



# Evidence for different bottom-up mechanisms in wood mouse (*Apodemus sylvaticus*) and bank vole (*Myodes glareolus*) population fluctuations in Southern Norway

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## Abstract

Animals that feed on forest tree seeds, such as *Apodemus* mice, increase in number after a mast year. At high latitudes, there is a similar delayed response by *Myodes* voles to high seed crops of bilberry (*Vaccinium myrtillus*), but here the mechanism is hypothesised to be increased forage quality, caused by a trade-off between reproduction and defence in the plants. Both *Apodemus* mice and *Myodes* voles eat berries, but only the latter feed on bilberry plants. Hence, only *Myodes* voles are predicted to respond to bilberry peak years. A second prediction is that the effect should last longer than any possible direct impacts of bilberries, because the plants would not be able to rebuild their defence until the succeeding summer. During a 21-year snap-trapping study of small rodents in Southern Norway, the spring population of bank vole (*Myodes glareolus*) was positively related to a bilberry seed index of the previous year, indicating increased winter survival, whereas the wood mouse (*Apodemus sylvaticus*) was not affected. Also the succeeding autumn population index of the bank vole was positively related to the bilberry index of the previous year, even when controlling for spring population levels. The wood mouse population responded to mast years of sessile oak (*Quercus petraea*), whereas seeds of Norway spruce (*Picea abies*) seemed to have some impact on both species. It is concluded that these rodents are mainly limited from below, but by different mechanisms for the granivorous and the herbivorous species.

**Keywords** Acorns · *Apodemus* · *Vaccinium* · *Myodes* · Seeds

## Introduction

Many animal species feeding on seeds/fruits of forest trees increase in number after a mast year, as a response to increased food supply. Well-known examples from the northern hemisphere include *Apodemus* mice that store acorns in autumn and which due to improved winter survival reach peak levels in the succeeding year (Watts 1969; Pucek et al. 1993; Shimada and Saitoh 2006). At high altitudes, there is a similar delayed relationship between seed production of bilberry (*Vaccinium myrtillus*) and *Myodes* voles feeding on this dwarf shrub in winter (Laine and Henttonen 1983; Selås et al. 2011),

but the causality is less obvious. Although winter food appears to be a limiting factor also for *Myodes* voles (Ylönen and Eccard 2004; Haapakoski and Ylönen 2013; Johnsen et al. 2017), bilberries cannot be stored in the same way as acorns, and at the start of the winter, there will be few bilberries left. Neither is it possible for voles, with their high metabolic rate, to gain fat reserves of importance for winter survival by eating berries in autumn.

For the bank vole (*Myodes glareolus*), both abundance and winter population declines have been related to food quality (Wereszczynska et al. 2007; Palo and Olsson 2009). Selås (1997) suggested that *Myodes* voles increase in number after years with high production of bilberries because they benefit from improved food quality, caused by a trade-off between reproduction and defence in the plants. According to the plant stress hypothesis, any stress factor that requires increased metabolic activity will force a plant to transfer complex proteins, which may act as feeding deterrents, to transportable and thereby easily digestible proteins (White 1984, 1993). The assumption is that protein is usually the limiting factor for

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herbivores and that not all plant proteins are available to them (e.g. Wallis et al. 2010). If the protein digestibility per time unit of a plant lies below the herbivore's critical threshold, then even a slight increase in the ratio of digestive to defensive (or unavailable) proteins may change the plant-herbivore interaction in favour of the herbivore, making the plant suitable as food. If this happens simultaneously in a plant population, the result will be a considerable temporal increase in the carrying capacity of herbivores feeding on this plant.

The plant stress hypothesis predicts that only small rodents feeding on dwarf shrubs should respond to a peak in berry production, whereas those feeding only on berries should remain more or less unaffected. Furthermore, the effect on the former group should last longer than any possible effects of nutrients provided by berries, because the plants will not be able to rebuild their chemical defence until the succeeding summer. These two predictions were supported in a study of bank vole and wood mouse (*Apodemus sylvaticus*) in Southern Norway during 1972–2000 (Selås et al. 2002). Both species eat berries (Hansson 1971), but only the bank vole feeds on bilberry plants, which are important as winter food (Hansson and Larsson 1978; Hansson 1985). However, the study lacked systematic field records of berry production and partly also estimates of relative rodent population levels in spring.

During 1999–2019, I trapped small rodents in spring and autumn in an area in Southern Norway where both bank vole and wood mouse are common. Bilberries were counted in late summer during 1999–2018. Here, I analyse the population fluctuation of these two species in relation to bilberry seed crops and mast years of two forest tree species. The main predictions were that only the bank vole should peak after a year with a high seed crop of bilberry, that the effect should last longer than what could be explained by berries as food and that only the wood mouse should peak after a year with a high seed crop of sessile oak (*Quercus petraea*). The prediction that wood mice should not respond to bilberries is similar to that of Selås et al. (2002), whereas the prediction that bank voles should not respond to acorns is based on the hypothesis that only wood mice are adapted to cope with the high tannin content in acorns of sessile oak (e.g. Shimada and Saitoh 2006).

## Material and methods

### Study area

The study area covers approximately 20 km<sup>2</sup> and is situated in Vegårshei Municipality, Aust-Agder County, in Southern Norway (58° 39'–58° 43'N, 8° 38'–8° 49'E, 150–300 m elevation). The climate is sub-oceanic with snow usually covering the ground from December through March or April. For

the normal period 1961–1990, the mean temperature in the coldest month, January, was –4 °C and in the warmest month, July, 15.5 °C. Forests make up approximately 80% of the landscape. The forests are characterized by a fine-grained mosaic of young, medium and old-aged coniferous, mixed and deciduous stands. Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), sessile oak, aspen (*Populus tremula*) and birch (*Betula* spp.) are the dominant tree species, and bilberry is a dominant dwarf shrub in old forest stands.

Common small rodent species in the study area are wood mouse, bank vole and field vole (*Microtus agrestis*). These three species are classified as granivorous, herbivorous-granivorous and herbivorous, respectively (Hansson 1971). The most common predators on small mammals are tawny owl (*Strix aluco*), long-eared owl (*Asio otus*), Tengmalm's owl (*Aegolius funereus*), pygmy owl (*Glaucidium passerinum*), common buzzard (*Buteo buteo*), red fox (*Vulpes vulpes*), pine marten (*Martes martes*), stoat (*Mustela erminea*) and weasel (*Mustela nivalis*). The latter two are regarded as specialist rodent predators, and 83% of my own observations ( $n = 18$ ) of these two species in the region of the study area were from years after a peak in small rodent numbers.

### Snap trapping of small rodents

Relative population indices of small rodents were obtained by the use of snap traps (type Rapp) baited with raw carrot. A total of 250 traps were put out each spring (early May) and autumn (late September), at 10 different sites in old forest stands with bilberry as the dominating plant in the field layer. Oak trees were not present in all plots, but always in close proximity. Old forests were selected because bank vole abundance is highest in forest habitats where the field layer is dominated by bilberry (Gorini et al. 2011). In young forests, the bilberry is usually less abundant. The wood mouse has been characterized as a habitat generalist (Diaz et al. 1999), and it is also more mobile than the bank vole (Bergstedt 1966). Hence, I regarded the selection of trapping sites to be less important for this species.

At each site, 25 traps were arranged ca. 5 m apart along a more or less straight line, depending on topography. Some sites had to be substituted during the course of the study due to timber logging, which reduced the coverage of bilberry. The traps were controlled and if necessary re-baited each day during a 4-day period, giving a total of ca. 1000 trap nights. The only exception was spring 2009, when the traps were set out for only two nights. I corrected the number of trap nights used for a given species by subtracting 0.5 trap nights for each trap that had captured another species, based on the assumption that these traps had been available on average half the time they were put out.

Removal sampling may affect the abundance and diversity of small mammals (Sullivan and Sullivan 2013), but I regard this as a minor problem when the main goal is to identify population peaks based on relative population indices in an area with high-amplitude population fluctuations. Besides, the fine-grained mosaic of the study area makes it easy for voles and mice to move between patches of preferred habitat. When also taking into consideration their high reproductive capacity, it seems likely that most individuals removed in May were replaced before snap trapping in September.

Usually, bank voles and wood mice do not reproduce in winter in Norway, so population changes from autumn to spring reflect winter survival. The aim of spring trapping was to obtain estimates of winter survival. Particularly in late autumn, bank voles and wood mice often enter buildings in the study area, sometimes in large numbers, indicating that surplus individuals move a lot in search for food then. Hence, rodents removed in September are probably most often replaced long before the trapping season in May. The immigrants may have lived in other habitats, but as surplus individuals, they are unlikely to be in better condition than the rodents that were removed. Hence, I assumed that the number present in spring mainly was a result of winter conditions in the trapping areas.

In some years, particularly wood mice may start reproduction very early, before snap trapping in May. Juveniles were omitted from the sample when calculating spring population indices used in the statistical analyses.

### Seed crops

From 1999 to 2018, I counted all bilberries in 15 fixed plots of  $2 \times 2 \text{ m}^2$ , situated in old forest stands of similar types as used for rodent trapping and spread out in the study area. For each plot, the berry production of each year was calculated as a proportion of the production in 1999, which I regarded to be a medium year. The annual berry production indices are thus the mean of all 15 plots. By this method, the plots are weighted equally, despite differences in overall berry production.

The only tree species that produce seeds of significant importance for small rodent winter survival in the study area are sessile oak and Norway spruce. As an index of seed crops of oak, I used the amount of acorns (metric tons) exported to Denmark from the municipalities Grimstad, Arendal and Froland, situated 10–50 km southwest of my study area and provided by the Norwegian Forest Seed Centre. This may not be a perfect index for acorn production (Selås 2016a), but during 2004–2018, it correlated well with the annual amount of acorns (range 0–20 l) collected from a selected reference oak tree close to my residence in the study area ( $r = 0.82$ ,  $P < 0.001$ ,  $n = 15$ ).

The annual spruce seed index, provided by the Norwegian Institute of Bioeconomy, is the proportion of 36–55 (mean 47)

spruce trees with medium or high cone crop at an intensively study research area in Birkenes Municipality, situated 50 km southwest of my study area (Andreassen et al. 2012). Mast years of Norway spruce usually occur simultaneously over vast areas (Nussbaumer et al. 2016), and for the period 1999–2007, there was a significant correlation between the cone index from Birkenes and a similar index calculated for a larger region consisting of Aust-Agder and the eastern neighbouring county Telemark (data from Timmermann 2008 and references therein;  $r = 0.84$ ,  $P = 0.008$ ,  $n = 9$ ).

### Snow-corrected winter temperature

A stable snow cover in winter is not a prerequisite for population peaks of small rodents in the study area. For instance, in 1998, there was an exceptional high population level in spring and summer of both bank vole and wood mouse (Selås et al. 2002), even though the mean snow depth at the closest meteorological stations did not exceed 10 cm in any of the preceding winter months (data from the Norwegian Meteorological Institute; eKlima.no). However, low temperatures in periods without an isolating snow cover may give increased mortality.

In a previous analysis of the population dynamic of the wood mouse in Aust-Agder, a snow-corrected winter temperature index appeared to explain at least some instances without expected peaks after oak mast years (Selås 2016a). I therefore used this index as an additional explanatory variable also in this study. For the first and last 15-day period of each winter month, the mean air temperature (if below zero) was corrected for mean snow depth by using a correction factor given by Algaard (1976). As an example, the correcting factor is 0.90 if the mean snow depth for the selected period is 10 cm and 0.12 if the mean snow depth is 50 cm. For these two cases, a mean air temperature of  $-10 \text{ }^\circ\text{C}$  would be corrected to  $-9$  and  $-1.2 \text{ }^\circ\text{C}$ , respectively. For each winter, I used the lowest 15-day corrected temperature in the analyses.

### Statistical analyses

I tested the relationships between rodent indices, calculated as number trapped per 100 trap nights, and seed indices in cross correlation analyses. Significant autocorrelations in the time series were corrected when calculating 95% confidence limits (Diggle 1990). Thereafter, I used the annual number of bank voles and wood mice trapped as response variables in GLM models (Poisson distribution and log link, corrected for overdispersion), with the log-transformed number of trap nights as offset. The explanatory variables were previous population indices, seed indices of the previous year and in models for rodent spring indices also the snow-corrected winter temperature. The software used was JMP®Pro 12.1.0 (SAS Institute, Cary, North Carolina).

## Results

The seed indices were not significantly correlated for the period 1999–2018 (bilberry–oak,  $r = 0.10$ ,  $P = 0.69$ ; bilberry–spruce,  $r = 0.31$ ,  $P = 0.20$ ; oak–spruce,  $r = 0.14$ ,  $P = 0.56$ ). Neither was the snow-corrected winter temperature correlated with any of the seed indices of the previous year (bilberry,  $r = 0.09$ ,  $P = 0.72$ ; oak,  $r = -0.24$ ,  $P = 0.30$ ; spruce,  $r = -0.04$ ,  $P = 0.88$ ).

During 1999–2019, a total of 2093 small rodents were trapped (Table 1), of which 56.0% were bank voles, 43.1% wood mice and 0.9% field voles. Spring population indices (adults trapped per 100 trap nights) of bank vole and wood mouse were not correlated ( $r = 0.04$ ,  $P = 0.864$ ), but there was a significant correlation for the autumn population indices ( $r = 0.49$ ,  $P = 0.030$ ; Fig. 1). For the wood mouse, there were 3 years (2005, 2007, 2014) when the trapping index of adults in spring was 3–6 times higher than the autumn trapping index of the previous year, which in all cases was an oak mast year (Table 1).

**Table 1** Number of small rodents trapped in Vegårshei, Southern Norway, and indices of seed crops of bilberry (B), sessile oak (O) and Norway spruce (S), 1999–2018

Year	Spring			Autumn			B	O	S
	Wood mouse	Bank vole	Field vole	Wood mouse	Bank vole	Field vole			
1999	0+0	0+0	0	2	1	0	1.00	12.90	0
2000	1+2	0+0	0	15	1	0	0.55	15.15	10
2001	2+0	2+0	0	19	23	0	0.85	23.78	0
2002	4+0	0+0	1	4	22	0	0.55	0.77	3
2003	3+0	4+0	0	47	40	0	1.09	17.47	0
2004	3+0	2+0	1	2	34	0	1.57	10.25	16
2005	10+7	23+0	0	109	110	2	0.78	0.44	0
2006	2+0	3+0	0	4	8	0	1.84	16.14	38
2007	26+18	5+0	2	151	66	0	0.66	2.32	0
2008	3+0	1+0	0	11	9	0	1.82	13.25	16
2009	9+0	3+0	1	128	69	0	1.88	0.48	4
2010	0+0	25+0	0	9	101	0	0.74	15.98	16
2011	4+0	24+1	0	13	34	0	0.46	10.90	15
2012	12+4	11+6	0	38	56	0	0.43	0.52	0
2013	1+0	3+0	0	3	23	0	1.38	13.13	0
2014	10+8	19+0	1	50	93	0	0.43	0	2
2015	0+0	1+0	0	4	11	0	1.42	1.11	38
2016	2+3	9+6	0	96	95	1	2.43	5.12	0
2017	1+0	29+0	3	14	161	4	0.78	6.89	0
2018	1+0	4+0	2	3	6	0	0.41	7.29	3
2019	2+1	5+0	0	41	24	0	–	–	–

For spring captures of wood mouse and bank vole, the data are given as adults + juveniles. The number of trap nights were approximately 1000 each spring and autumn, except from spring 2009, when it was only 500

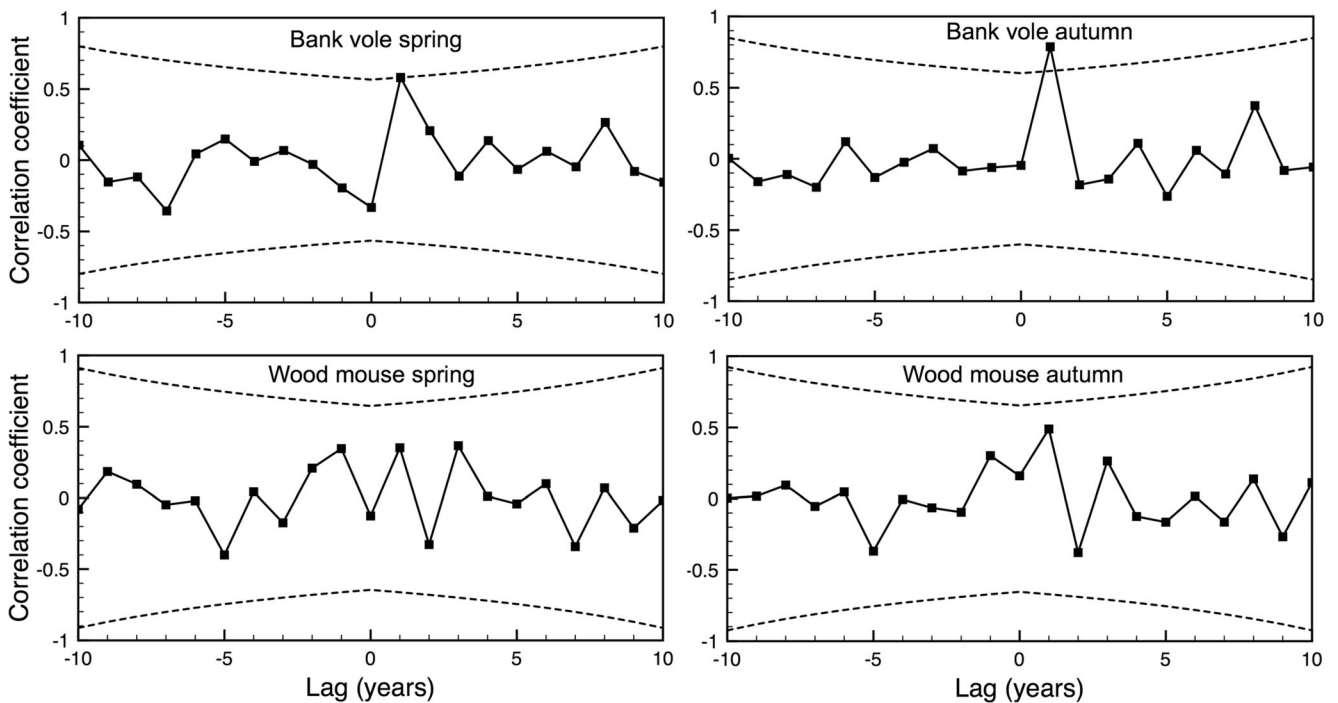
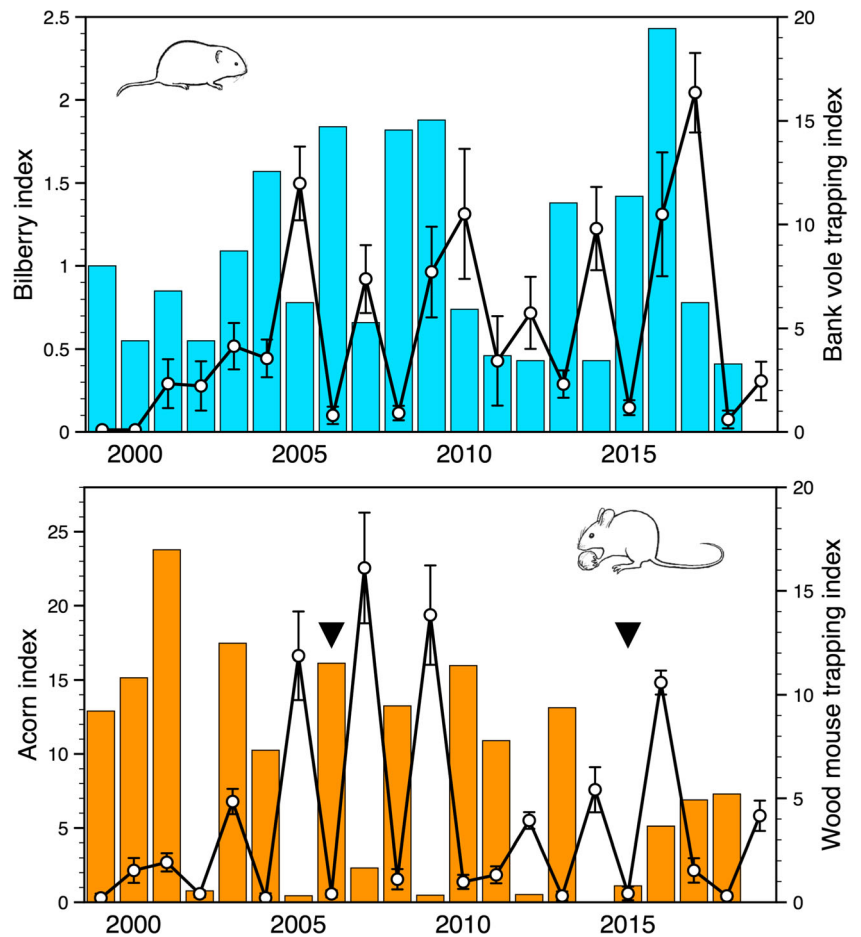
Cross-correlation analyses showed a significant positive relationship with the bilberry index, with a 1-year time lag, for both spring and autumn population indices of bank vole (Fig. 2). No significant correlations were found for the wood mouse (Fig. 2). A similar analysis with spruce seeds gave the opposite result, a significant positive correlation at lag one for spring and autumn indices of wood mouse only. In the cross-correlation analyses between the acorn index and the rodent indices, no significant correlations were found. When restricting the analysis to the shorter period with acorn counts from the reference tree in the study area, 2004–2018, there was a significant positive correlation with a 1-year lag for the wood mouse spring index, whether the index based on the reference tree or the acorn export index was used. This was mainly because the “delayed response” in 2001–2003 (Fig. 1) was omitted then.

There were 7 years with a high seed crop of bilberry, and they were all followed by a year with high bank vole numbers (Fig. 1). Acorns and spruce seeds were scarce in only two of the bilberry peak years, 2009 and 2016 (Fig. 1). In the succeeding years, 2010 and 2017, there were high numbers of bank vole only, and not of wood mouse (Fig. 1). Although the wood mouse population was expected to peak after mast years of oak or spruce, it did not respond to the oak mast years 2001 and 2010 (Fig. 1). The winters 2001/2002 and 2010/2011 had the lowest snow-corrected 15-day temperature during the study period,  $-5.2$  and  $-4.1$  °C, respectively. The third lowest value was  $-2.5$  °C in 2000/2001.

In GLM models, the spring population index of bank vole was positively, but not significantly, related to the autumn population index of the previous year ( $\chi^2 = 1.08$ ,  $P = 0.300$ ). In contrast, the wood mouse spring index showed a negative relationship with the previous year’s autumn index ( $\chi^2 = 4.16$ ,  $P = 0.041$ ). For the bank vole, there was a significant positive relationship with the bilberry index of the preceding year (Table 2), but not with acorns or spruce seeds ( $\chi^2 < 0.3$ ,  $P > 0.6$ ), nor with the snow-corrected winter temperature ( $\chi^2 = 0.27$ ,  $P = 0.602$ ). For the wood mouse, there was a significant positive correlation with acorns ( $\chi^2 = 4.88$ ,  $P = 0.027$ ) and spruce seeds ( $\chi^2 = 12.11$ ,  $P < 0.001$ ), but not with bilberries ( $\chi^2 = 2.55$ ,  $P = 0.110$ ) or the snow-corrected temperature ( $\chi^2 = 1.18$ ,  $P = 0.277$ ). In a multiple model, however, also the corrected winter temperature index contributed significantly, together with acorns and spruce seeds (Table 2).

The number of rodents trapped in autumn was strongly related to the spring population indices (bank vole,  $\chi^2 = 30.13$ ,  $P < 0.001$ ; wood mouse,  $\chi^2 = 14.21$ ,  $P < 0.001$ ). When controlling for the impact of spring indices, both the bilberry index and the spruce seed index of the previous year contributed significantly for the bank vole, whereas only the spruce seed index contributed for the wood mouse (Table 3). In these models, the explanatory power of both spring population indices and seed indices were reduced compared to the

**Fig. 1** Number of bank vole and wood mouse trapped per 100 trap nights in autumn at ten study sites in Vegårshei, Southern Norway (mean  $\pm$  SE), in relation to seed crops of bilberry and sessile oak, respectively (bars). Years with heavy cone crops of Norway spruce (Table 1) are indicated by filled triangles in the wood mouse panel



**Fig. 2** Cross-correlation coefficients calculated between the bilberry index and the bank vole spring index, the bank vole autumn index, the wood mouse spring index and the wood mouse autumn index. The 95% confidence limits, corrected for autocorrelations, are given as dotted lines

**Table 2** Results from GLM models (Poisson distribution and log link, corrected for overdispersion) with the total number of adult bank vole and wood mouse trapped in spring year  $t$  (2000–2019) as response variables and the log-transformed number of trap nights as offset

Explanatory variable	Estimate	SE	df	$\chi^2$	$P$
<b>Bank vole</b>					
Intercept	−1.986	0.496	1		
Bilberries, $t-1$	0.958	0.317	1	8.73	0.003
<b>Wood mouse</b>					
Intercept	−2.318	0.390	1		
Acorns, $t-1$	0.091	0.026	1	14.30	<0.001
Spruce seeds, $t-1$	0.041	0.009	1	18.72	<0.001
Winter temperature	0.341	0.131	1	7.93	0.005

Explanatory variables are seed crops of the previous year and a winter temperature index corrected for snow depth. Only significant variables are included in each model

univariate tests, because of the positive correlation between them. The acorn index, however, was not a significant predictor for autumn numbers of any of the two rodent species even in univariate tests ( $\chi^2 < 1.0$ ,  $P > 0.4$ ), unless the index based on the reference tree from the shorter period 2004–2018 was used. Then there was a significant effect in the univariate test for the wood mouse ( $\chi^2 = 5.54$ ,  $P = 0.019$ ).

The proportion of juvenile bank voles in spring was positively related only to the spruce seed index of the previous year ( $R^2 = 0.30$ ,  $P = 0.018$ ). There was a similar tendency for the wood mouse ( $R^2 = 0.20$ ,  $P = 0.062$ ), but for this species, a low combined population index of wood mouse and bank vole in the previous autumn was the best predictor for a high proportion of juveniles among mice trapped in spring ( $R^2 = 0.32$ ,  $P = 0.14$ ). Spruce seeds did not contribute significantly in a multiple model.

**Table 3** Results from GLM models (Poisson distribution and log link, corrected for overdispersion) with the total number of bank vole and wood mouse trapped in autumn year  $t$  (2000–2019) as response variables and the log-transformed number of trap nights as offset

Explanatory variable	Estimate	SE	df	$\chi^2$	$P$
<b>Bank vole</b>					
Intercept	−0.485	0.247	1		
Spring index, $t$	0.410	0.118	1	11.65	<0.001
Bilberries, $t-1$	0.559	0.193	1	8.90	0.003
Spruce seeds, $t-1$	0.019	0.007	1	6.25	0.012
<b>Wood mouse</b>					
Intercept	−0.144	0.268	1		
Spring index, $t$	0.393	0.212	1	3.86	0.049
Spruce seeds, $t-1$	0.037	0.015	1	4.73	0.030

Explanatory variables are spring population indices (number trapped per 100 trap nights) and seed crops of the previous year. Only significant variables are included in each model

## Discussion

All years with a high production of bilberries were followed by a year with high numbers of bank vole, whereas the wood mouse responded only to acorns and spruce seeds. Only the bank vole population increased after two instances with high berry production but few acorns and spruce seeds. The same pattern was observed in the 1970s; the peaks in bilberry seed crops in 1972 and 1977, when acorns and spruce seeds were almost absent, were both followed by a peak in bank vole numbers but a drop in the number of wood mouse (Christiansen 1983; Selås et al. 2002). Predators may modulate herbivore population fluctuations (White 2013), but the temporal asynchrony of bank vole and wood mouse related to asynchronous seed production of bilberry and sessile oak in Southern Norway suggests that top-down effects are not strong contributors to rodent fluctuations here.

Also the prediction of a prolonged effect on bank vole performance was supported. Both spring and autumn population indices were positively related to the berry production in the previous year, the latter even when spring population levels were controlled for. Bilberries are not stored by voles (Hansson 1971), and at the start of the winter, there are few berries left. Hence, the pattern found here can hardly be explained by nutrients provided by berries, as suggested for a similar relationship between berry production and population levels of the northern red-backed vole (*Myodes rutilus*) in southwestern Yukon (Krebs et al. 2010).

Prior to my study, the bank vole population exhibited a more cyclic fluctuation pattern in Aust-Agder (Selås et al. 2002). Less cyclic fluctuations during the last 20 years are related to a less cyclic production of bilberries, which again are linked to climate (Selås et al. 2015). During 1999–2006, the bank vole population in Aust-Agder did not fluctuate in synchrony with bank vole populations in Hedmark County, eastern Norway (Wegge and Rolstad 2018; Framstad 2019), but thereafter the populations peaked in the same years: 2007, 2010, 2014 and 2017. The climate thus appeared to act as a stronger synchronizing factor for bilberry reproduction in the last period. According to newspaper interviews with the author of a book about wild berries in Norway, Øyvind Stranna Larsen (e.g. Aftenposten 20 July 2016), there was an exceptional high production of bilberries in most parts of South Norway in 2013 and 2016. These years were peak years also in large parts of Sweden (Langvall and Dahlgren 2016). Accordingly, bank vole populations peaked in 2014 and 2017 in several parts of both Norway (Wegge and Rolstad 2018; Framstad 2019) and Sweden (Ecke and Hörnfeldt 2018).

As expected from the high berry production in South Norway in 2013, Johnsen et al. (2017) observed high survival of bank voles in all plots in their study area in Hedmark County in winter 2013/2014, regardless of whether

supplemental food was added or not. In the succeeding winter 2014/2015, there was high winter survival only in plots that received supplemental food. Also for other herbivorous rodent species, there is increasing support for the importance of food quality (Massey and Hartley 2006; Erlinge et al. 2011; Forbes et al. 2014a, b; Wiczorek et al. 2015). At least at higher latitudes, the common pattern is that populations of both *Microtus* voles and lemmings often, but not always, peak simultaneously with *Myodes* vole populations (e.g. Krebs et al. 2002; Korpimäki et al. 2005; Ecke et al. 2017; Wegge and Rolstad 2018; Framstad 2019). A suggested mechanism is that flowering and seed production of some plant species grazed by *Microtus* voles and lemmings are more or less synchronized by the same weather factors that determine the production of bilberries (Selås 2016b). At higher altitudes and latitudes, plants may also be stressed or synchronized by cosmic ray fluxes, which depends on large-scale physical factors like temperatures, air pressure and solar and lunar cycles (De Mendonca et al. 2013; Selås 2014).

The response of the two rodent species in my study could be expected given that both species eat spruce seeds, but only bank voles digest bilberry plants, and only wood mice are able to cope with the high tannin content in acorns of the sessile oak (e.g. Onodera et al. 2017). A positive effect of spruce seeds on spring population levels of wood mouse but not bank vole is probably an artefact. The production of spruce seeds had a marked peak in 2006 and 2015. In both years, there was also a rich berry production, which may have masked any additional effects of high spruce seed abundance on the bank vole population. Acorns, on the other hand, were abundant only in 2006, making the impact of spruce seeds on the wood mouse population very visible in 2015–2016.

Acorns apparently improved wood mouse winter survival, but not reproduction. The reason is probably that the tannin content in acorns of sessile oak in Norway is so high that they do not offer sufficient nutrients for reproduction. When it comes to the lack of wood mouse peaks after some oak mast years, low winter temperatures are one possible explanation. However, given that wood mice cannot survive solely on acorns with high tannin content (Shimada et al. 2006), also overexploitation of important alternative food sources due to high rodent numbers in the mast year, as was the case in 2010 (peak year for bank vole), has been suggested to prevent population peaks (Selås 2016a).

When controlling for seed crops of the previous year, spring population indices of bank vole and wood mouse were not significantly related to previous autumn population indices. The removal trapping in autumn may have had some influence on the results, but the most likely explanation is that autumn population levels in most (but not necessarily all) years were higher than the winter carrying capacities set by winter food supply. After some oak mast years, 3–6 times as many adult wood mice were trapped in spring as in the

previous autumn. A possible explanation is that wood mice are less likely to encounter the traps in oak mast years because they spend much time storing acorns then and less time searching for alternative food. Oak masting is usually a regional phenomenon, so immigration from nearby areas without acorns is less likely to be the cause.

To conclude, population peaks of both wood mouse and bank vole in Southern Norway can be interpreted as responses to temporal increases in carrying capacity related to food supply, although the mechanisms seem to be different. The explanation for the relationship between masting of forest trees and population peaks of partly or entirely granivorous rodents, such as the wood mouse, is well-known and acknowledged (e.g. Jensen 1982; Wolff 1996; Falls et al. 2007; Ogawa et al. 2017; Sullivan et al. 2017). In contrast, a possible relationship between changes in food quality and the performance of herbivorous rodents cannot be observed directly and is thus less obvious. So far, the main support for the plant stress hypothesis (White 1984, 1993) as an explanation for vole population fluctuations in Norway seems to be the relationship between bilberry seed crops and the abundance of *Myodes* voles and other herbivores that feed on this plant species (Selås et al. 2011; Selås 2019).

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## Compliance with ethical standards

**Conflict of interest** The author declares that he has no conflict of interest.

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